



Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

WHY POLAR BODIES DO NOT DEVELOP

By Edwin G. Conklin

DEPARTMENT OF BIOLOGY, PRINCETON UNIVERSITY

Presented to the Academy, August 3, 1915

Since the work of O. Hertwig (1890) and Boveri (1891) it has been known that the two small cells which are formed at one pole of the egg during its maturation divisions and which have long been known as 'polar bodies' since they mark out the 'animal' or ectodermal pole of the egg are homologous with cells which in the male give rise to functional spermatozoa, so that the polar bodies are generally recognized as small and non-functional egg cells, a view which was first set forth by Mark (1881). Before the two maturation divisions which lead to the formation of eggs or spermatozoa the sex cells are called 'oöcytes' in the case of the female, 'spermatocytes' in the case of the male; after the first maturation division they are called 'second oöcytes' or 'second spermatocytes' and after the second maturation division they are known as 'oötids' or 'spermatids.' In the case of the male both of these divisions are equal and all of the spermatids may become functional spermatozoa, in the female both maturation divisions are usually very unequal the smaller division product in each case being the 'polar body,' and the larger the 'egg.'

In many animals the maturation divisions of the egg may be made approximately equal by pressure or by centrifugal force so that the difference in size between the polar body and the egg largely disappears. Thus if the eggs of the gastropod *Crepidula plana* are subjected to a centrifugal force of about 600 times gravity during the first or second maturation divisions some of the eggs in which the axis of centrifuging coincides with the axis of the division figure, or spindle, divide into approximately equal halves. In my experiments on the eggs of *Crepidula* the giant polar body is usually the second one since the eggs were centrifuged in most cases during the second maturation division; when the centrifuging occurred during the first maturation the first polar body is the giant one; when it occurred during both maturation divisions both polar bodies are abnormally large. Nevertheless only one of these cells develops.

In this animal the spermatozoon always enters the egg during the first maturation division and usually at the pole opposite that at which the polar bodies normally lie. In normal cases therefore the spermatozoon is always found in the 'egg' or larger daughter cell and never

in the polar body; and even when the two daughter cells are made equal by pressure or by centrifugal force the spermatozoon always lies in one daughter cell and not in the other. The same is true if the centrifugal force is applied during the second maturation division; although the daughter cells may be equal in size the spermatozoon is found in only one of these cells. Subsequent events show that only that cell develops which contains the spermatozoon.

In *Crepidula* and many other mollusks as well as in annelids and ascidians the spermatozoon normally enters the egg at the beginning of the first maturation division and always before the first polar body is cut off. Indeed the first maturation spindle will usually remain in the metaphase, or middle stage of division, until a spermatozoon enters or until the egg is stimulated by other means (artificial parthenogenesis) to begin development. As soon, however, as a spermatozoon enters an egg the maturation division proceeds and the whole process of development is set in motion in the cell which contains the spermatozoon. But the polar bodies, which do not contain the spermatozoon, never develop even though they may be as large as, or even larger than, the egg which does develop.

The giant polar bodies of *Crepidula* resemble unfertilized eggs in that the cytoplasm remains diffused throughout the whole cell whereas in eggs after fertilization there is a fairly sharp separation of cytoplasm and yolk. Associated with this lack of segregation of cell substances there is also a lack of distinct polar differentiation in giant polar bodies. The intra-cellular movements which lead in the fertilized egg to the segregation of cytoplasm at the animal pole and of yolk at the vegetative pole do not take place in giant polar bodies.

These giant polar bodies invariably contain a nucleus and they may contain samples of all the substances found in the egg; they may contain most of the protoplasm of the egg; they may be larger than the cell which does develop but the one thing which they lack is a spermatozoon, whereas the egg cell which does develop invariably contains a spermatozoon. We must conclude therefore that the giant polar bodies of *Crepidula* do not develop because they do not contain a spermatozoon.

The failure of normal polar bodies to be fertilized and to develop is generally held to be due to their small size, but even when these polar bodies are large as is sometimes the case in mollusks, polyclads and nematodes they do not undergo fertilization and do not develop though they sometimes divide once or twice. In one case only has the development of a polar body, or rather of both second oöcytes, been observed.

Francotte (1898) discovered in the polyclad *Prostheceraeus* that at the first maturation the egg sometimes divided into two nearly equal cells; each was then entered by a spermatozoon and normally fertilized and at the second maturation division each formed a small second polar body and the larger cells then underwent normal cleavage and developed to the gastrula stage. In a few other instances the entrance of a spermatozoon into a polar body has been reported though some of the cases are not entirely convincing and need verification. Thus Platner (1886) described the entrance of a spermatozoon into a polar body of *Arion*; he maintained that the polar bodies are formed before the entrance of the sperm, which would make this case similar to that of *Prostheceraeus*, but the evidence is by no means conclusive. Sobotta (1895) calls special attention to the large size of the polar bodies in the mouse and suggests that they may be capable of being fertilized but offers no evidence in favor of this view. Kostanecki (1897) has observed a spermatozoon with its head penetrating the second polar body of *Physa*, a thing which he regards as merely a 'curiosity.'

Lefevre (1907) observed that the polar bodies of *Thalassema* undergo several cleavages resulting in the formation of a morula-like cluster of minute cells when they are exposed to weak solutions of HCl; "thus they respond to the same divisional stimulus supplied by the acid solutions as does the egg cell itself."

The most striking difference between *Prostheceraeus* and other animals in which giant polar bodies have been reported is to be found in the fact that in the former fertilization does not take place until after the first maturation division is completed and then each of the daughter cells is fertilized, whereas in the latter the entrance of the spermatozoon occurs before the completion of the first maturation division with the result that one of the daughter cells contains a spermatozoon and the other does not.

In this fact is to be found the explanation of the different behavior of the giant polar bodies of *Prostheceraeus* and of *Crepidula*, for it is well known that one of the first effects of the entrance of a spermatozoon into an egg is the prevention of other spermatozoa from entering. If the spermatozoon enters the egg before the first polar body is cut off that polar body as well as other cells which are formed later from the egg are rendered "immune" to other spermatozoa.

But although the influence of the entering spermatozoon spreads so rapidly over the egg that within a few minutes at most it renders all portions of the egg surface 'immune' to other spermatozoa and thus prevents the fertilization of polar bodies which are formed after fertili-

zation, this influence does not go so far as to cause the polar bodies to develop, even though such polar bodies may be formed several hours after the spermatozoon enters the egg. In *Crepidula* the second polar body is formed about three hours after the entrance of the spermatozoon into the egg, and during this time the sperm head has grown into a vesicular nucleus and the sperm aster has become quite large, but in spite of this the spermatozoon has not sufficiently affected the egg substance to cause the second polar body to develop even though that body may contain the larger part of the egg protoplasm. Only that portion of the egg develops, in such cases, in which the sperm nucleus and aster are present.

This conclusion is similar in many respects to that reached by Zeigler (1898) who found that when eggs of the sea urchin, *Echinus microtuberculatus*, were constricted by cotton fibers under pressure only that portion of the egg which contained the sperm segmented while the portion containing the egg nucleus never divided, though its nucleus frequently went through the division phases, but without any division resulting. In this case the portion of the egg containing the sperm might remain for some time connected with the other portion by a narrow neck, and yet the influence of the sperm in the one half did not cause the other half to develop.

These facts are of interest because of their bearing on the nature of one of the processes concerned in fertilization. In a series of important and extensive works on artificial parthenogenesis and fertilization which he has summarized in a recent book Loeb (1909) has shown that at least two factors are involved in artificial parthenogenesis, (1) an external factor, such as butyric acid, which causes a cytolysis of the cortical layer of the egg followed by increased oxidation and which leads to the rapid disintegration of the egg at normal temperatures, and (2) an internal factor, such as hypertonic solutions, lack of oxygen, etc., which inhibits this disintegration. Loeb concludes that in normal fertilization also both of these factors are present and that the spermatozoon carries substances into the egg which (1) cause cytolysis of the cortical layer and increased oxidation and also other substances which (2) inhibit this cytolysis before it leads to the disintegration of the egg.

My experiments on the giant polar bodies of *Crepidula* show that changes in the cortical layer which prevent the entrance of a second spermatozoon take place very rapidly over the entire egg, but that the spermatozoon which enters does not cause any portion of the egg to develop except the cell in which it lies. Although the spermatozoon enters the egg of *Crepidula* about three hours before the formation of

the second polar body the influence of the spermatozoon on the egg protoplasm during this time is not sufficient to start development in the second polar body even though it may contain the greater part of the egg substance.

This indicates that the second factor concerned in the process of normal fertilization is not to be found in the diffusion through the egg of some chemical substance carried in by the spermatozoon but is some non-diffusable substance, probably an organic structure.

Long ago Boveri (1887) showed that under certain circumstances the egg of *Ascaris* may divide at the first cleavage so that half of the egg nucleus passes into each daughter cell while the sperm nucleus does not divide but goes entire into one of the first two cells. Such a condition he called 'partial fertilization,' and in such cases he found that both halves of the egg develop, thus showing that the activating influence of the spermatozoon has affected both halves. Since in this case the centrosome is the only structure derived from the spermatozoon which is known to go into both cleavage cells he reached his well known conclusion that the essential thing in fertilization is the addition of a centrosome to the egg cell.

It is possible of course that other unrecognized structures are introduced by the spermatozoon and serve to activate the egg. Meves (1911) found that the spermatozoon of *Ascaris* introduces into the egg a number of coarse granules, the 'plastochondria,' which he thinks unite with similar granules in the egg and are then distributed to the cleavage cells. However, in one of the Echinids he finds that the large granule or 'plastosome' which is derived from the middle-piece of the spermatozoon goes into one only of the first two cleavage cells and yet both develop. I have found that the 'plastosomes' in the eggs of gastropods and ascidians may be distributed very unequally to the first two cleavage cells without interfering with the further division of both cells, and there is no evidence whatever that the activating influence of the spermatozoon is due to these granules.

On the other hand many investigators have held that fertilization is essentially a chemical process and that the activation of the egg depends upon the introduction by the spermatozoon of certain chemical substances which diffuse through the egg.

The observations recorded in this paper indicate that the second or internal factor in normal fertilization is a non-diffusable substance which is introduced by the spermatozoon, and they strongly suggest that this factor is the sperm centrosome, a position which Boveri has long maintained and which I have hitherto contested.

In conclusion, giant polar bodies do not develop because they are not fertilized and they are not fertilized because they are generally formed after a spermatozoon has entered the egg and has rendered it impervious to other spermatozoa.

REFERENCES

- Boveri, Th. (1887). Ueber den Anteil des Spermatozoon und der Teilung des Eies. *München, SitzBer. Ges. Morph.*, 3.
 (1891). Befruchtung. *Merkel u. Bonnet Ergebnisse* 1.
 Francotte, P. (1898). Recherches sur la maturation, la fecondation et la segmentation chez les Polyclads. *Arch. zool., Paris*, 6.
 Hertwig, O. (1890). Vergleich der Ei- und Samenbildung bei Nematoden. *Arch. mikr. Anat., Bonn*, 36.
 Kostanecki, K. (1897). Ueber die Bedeutung der Polstrahlung, etc., *Ibid.*, 49.
 Lefevre, G. (1907). Artificial Parthenogenesis in *Thalassema mellita*. *J. Exp. Zool.*, 4.
 Loeb, J. (1913). Artificial Parthenogenesis and Fertilization, Chicago.
 Mark, E. L. (1881). Maturation, Fecundation and Segmentation of *Limax Compestris*. *Bull. Mus. Comp. Zool. Harvard*, 6.
 Meves, Fr. (1911). Ueber die Beteiligung der Plastochondrien an der Befruchtung des Eies von *Ascaris megalocephala*. *Arch. mikr. Anat.*, 76.
 (1912). Verfolgung des sogenannten Mittelstückes des Echinindenspermiums im befruchteten Ei, etc. *Ibid.*, 80.
 Platner, G. (1886). Ueber die Befruchtung von *Arion Empiricorum*. *Ibid.*, 27.
 Sobotta, J. (1895). Die Befruchtung und Furchung des Eies der Maus. *Ibid.*, 40.
 Ziegler, H. E. (1898). Experimentelle Studien ueber die Zellteilung. *Arch. Entw. Mech., Leipzig*, 6.

RADIAL VELOCITIES OF THE PLANETARY AND IRREGULAR NEBULAE

By W. W. Campbell and J. H. Moore

LICK OBSERVATORY, UNIVERSITY OF CALIFORNIA

Presented to the Academy, September 10, 1915

In a former number of the PROCEEDINGS¹ one of the authors presented results on the radial velocities of 54 gaseous nebulae determined by spectrographic methods at the Lick and D. O. Mills Observatories, working respectively in the northern and southern skies. It was there shown that the planetary nebulae, or those of regular form, are rapid travelers in comparison with the stars, a fact which casts serious doubts upon the generally accepted hypothesis that the stars have been formed from planetary nebulae by processes of evolution.

During the past year observations at both institutions have been extended to fainter members of this class of objects, and there are now available some 348 measures of the velocities of approach and recession of 92 gaseous nebulae, or those whose spectra are composed of bright lines.